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Wildlife response to recreational trail building: An experimental method and Appalachian case study

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ABSTRACT

Trail networks are common infrastructure in protected areas for visitors to exercise, connect with nature, and learn about natural and cultural resources. However, there are concerns that the presence and construction of trails affect the quality of wildlife habitats, extending human disturbance into secluded areas. In this study, we developed a before-after control-impact experimental design to investigate the impacts of new trail construction on six terrestrial vertebrate species in an Appalachian protected area in the U.S. Using camera traps, we monitored animal use of the study area before, during, and after construction, on the trail, near the trail, and at a control site. Our results indicate statistically significant impacts of trail building and presence on four common species. During trail construction, white-tailed deer (*Odocoileus virginianus*) and coyotes (*Canis latrans*) decreased their activity on and/or near the trail, while raccoons (*Procyon lotor*) increased activity on the trail. These three species returned to the area at pre-building levels once trail construction was complete. After trail building, eastern gray squirrel (*Sciurus carolinensis*) showed decreased use of the trail area. We also observed altered timing of daily activity patterns for squirrels and deer, both diurnal species. Deer activity became more spread throughout the day within the near-trail zone during construction. After the trail was complete, squirrels shifted activity to earlier in the day, after sunrise and prior to the peak of recreational activity. We conclude that while trail building may alter habitat quality for some species, this mostly occurred during the construction phase, and was fairly minor for our study species. To minimize impacts, we suggest that trail building be restricted to a short time period during a season when species of concern are least sensitive. Our use of control sites allowed us to distinguish experimental effects from natural population fluctuations, and should serve as a foundation for future work investigating the effects of trails and other linear human disturbances on wildlife communities, especially in sensitive habitats and ecosystems.

1. Introduction

Protected areas are set aside from development to conserve natural ecosystems for ecological and social benefits. Most of these areas allow public access and provide recreation opportunities. While recreation in natural settings is an important cultural ecosystem service of many protected areas, human activities can alter ecosystems (Knight & Cole, 1991; Liddle, 1997). Trails are a key infrastructure for recreation and nature-based tourism, both providing access to natural areas and concentrating recreational activity to a small footprint of disturbance (Leung & Marion, 1999). Nearly every protected area has trails; even those classified as "Strict Nature Reserves" by the International Union for Conservation of Nature contain this infrastructure (Dudley, 2008). The percentage of visitors to protected areas that use trails is high worldwide (60%–87%), and vary with trail quality (Blotkamp, Meldrum, Morse, & Hollenhorst, 2010; Department for Environment & Heritage, 2008; Reed et al., 2008). Recreation trails continue to be built, maintained, and re-routed in nature conservation areas worldwide. For example, trail mileage in U.S. state and federal lands increased by 43 % between 1965 and 2015, a total increase of over 214,500 km of trails (American Hiking Society, 2015).

Recreational trails can alter landscapes in ways that affect local wildlife species. For example, trails create edge habitats, can aid the spread of invasive plant species (Hammitt, Cole, & Monz, 2015), change hydrological patterns (Sutherland, Bussen, Plondke, Evans, & Ziegler, 2001), alter the composition and structure of soil and vege-

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tation communities (Ballantyne & Pickering, 2015), and lead to habitat fragmentation (Marion, Leung, Eagleston, & Burroughs, 2016). Shifts in physical, vegetative, and microfauna community structures contribute towards habitat alteration and might be exhibited in the terrestrial vertebrate community on a local scale. For example, small mammals that prefer dense understory, such as some voles, shrews, and squirrels, may be locally displaced by trail construction if vegetative cover removed provided quality habitat or predator shelter (Negro, Isaia, Palestrini, & Rolando, 2009; Rolando, Caprio, & Negro, 2013; Tounzen, Epperson, & Taulman, 2012). Specifically, eastern gray squirrels (*Sciurus carolinensis*) are widely known to prefer areas with abundant understory vegetation (Tounzen et al., 2012), such as that removed along a new trail corridor. Trail construction may also attract species whose food source is enhanced by aspects of the construction process, such as raccoons (*Procyon lotor)* feeding on invertebrates and mast (Owen, Berl, Edwards, Ford, & Wood, 2015), made readily available in freshly upturned soils. Raccoons are also known to be attracted to forest edge habitats (Barding & Nelson, 2008), and may thus be attracted to trails that have edge habitat qualities. Because trail work, like recreation activities, typically occurs during daylight hours, we expect diurnal species sensitive to human presence to be more affected than nocturnal species during trail construction.

Past research has shown species-specific effects of the trail structure on terrestrial wildlife, with some species preferring to use human trails while others avoid them. Large predators such as felids, canids, and sometimes ungulates, are sometimes found to prefer using trails (Coppes, Burghardt, Hagen, Suchant, & Braunisch, 2017; Cusack et al., 2015; Harmsen, Foster, Silver, Ostro, & Doncaster, 2010; Karanth & Nichols, 1998). However, some of these same species are found to alter daily activity patterns in areas with recreation, avoiding humans in real time (e.g., coyotes, gray foxes, mule deer, white-tailed deer, elk, and wolves: Barrueto, Fort, & Clevenger, 2014; Nix, Howell, Hall, & McMillan, 2018; Reilly, Tobler, Sonderegger, & Beier, 2017; Rogala et al., 2011). Prey species are sometimes attracted to busier trails, such as ungulates in the Rocky Mountains (Muhly, Semeniuk, Massolo, Hickman, & Musiani, 2011) while the same species can be displaced by recreational activity in other cases, such as elk in eastern Oregon (Wisdom et al., 2018). In the eastern U.S., the largest-scale empirical study to date on mammalian activity in relation to human-made trails found that most species studied did not avoid trails, and predator species positively selected them, specifically at night (Kays et al., 2016). A trail structure could lead to long-term changes in predator-prey dynamics, even if human use is minimal (Berger, 2007; , J.R. Miller and Hobbs, 2000; Muhly et al., 2011; Shannon, Cordes, Hardy, Angeloni, & Crooks, 2014). Such alterations to wildlife behavior corresponding to nature-based recreation can have cascading effects in the greater ecosystem at larger spatial scales. With the continued increase in recreation demand overlapping with conservation efforts in protected areas, it is critical to take the next step in determining the causality of recreation-related human activity such as trail building on wildlife activity.

Due to the difficulty of implementing manipulative experiments in natural settings, most ecology and wildlife studies rely on correlational designs to test hypotheses, and thus have limited ability to infer causation. However, the construction of new infrastructure in protected areas offers an opportunity to evaluate the impact of human disturbance on wildlife within an experimental framework. For example, a suite of studies examined the impact of construction of a new paved path in Grand Teton National Park. American black bears (*Ursus americanus*) altered their activity patterns to avoid zones and time periods of high human use after the construction of the paved path (Costello, Cain, Nielson, Servheen, & Schwartz, 2013), while ungulate species reduced their anti-predator behavior near the paved path, effectively using human presence as a shelter from predators (Shannon et al., 2014). Two species of breeding sparrows, which nest on the ground or in low shrubs in this sagebrush ecosystem, also avoided the new path area, while nests remaining near the path had increased success rates (Chalfoun, 2011). Together, these findings provide strong evidence for the human shield hypothesis (Berger, 2007; Muhly et al., 2011), with both predator and prey changing habitat use after the construction of a recreation trail as compared with the period prior to construction. By using a before-after control-impact (BACI) experimental design, these studies were able to draw stronger conclusions about the cause and effect of relationships they discovered.

Despite the constant creation and maintenance of trails in protected areas globally, few studies have investigated the impacts of trail construction on wildlife, and even fewer have used an experimental design towards these aims. In this study, we developed a method that can be used to fill these two gaps in the research, and present results from a case study in the Appalachian Mountains that test two hypotheses regarding how trail building and trail presence would affect the Appalachian study species. We predict that effects would be strongest along the trail during construction, diminishing somewhat with distance from the trail. We also hypothesized that the activity level and presence of species sensitive to human activity would remain reduced during the first few months that the trail was open to recreation, and that species that showed significantly altered activity levels and presence would also have significantly altered daily activity patterns in the treatment zones. Based on the results of our case study, we identified patterns in six common species' responses to trail construction and the recreational trail structure, to inform future trail construction and improvement projects in forested regions. While our before-after control-impact (BACI) study had measurements from 7045 camera nights across 301 camera deployments at 63 camera sites, these were used to evaluate only a single treatment, one newly built trail (Hurlbert, 1984). This lack of treatment replication is typical for landscape-scale experiments in which replication is often difficult, impossible, or impractical (Colegrave & Ruxton, 2018; Davies & Gray, 2015; Oksanen, 2001). While more replicates would help establish the generality of our results, we believe that our use of BACI comparisons provides a useful measure of the response of our study species to the treatment of mechanized trail building, and hope this will encourage others to extend this work with additional experiments.

2. Methods

In this study we designed and implemented a BACI experiment to address our research question regarding the local effects of motorized trail building and the presence of a new unpaved recreational trail on common terrestrial vertebrates. To address our research question and hypotheses, we modeled occupancy to represent presence, and detection frequency to represent activity level of six study species to compare their spatial distribution and intensity of habitat use before, during, and after trail building. We also analyzed the daily activity patterns of our study species during and after trail building, comparing treatment zones to the control zone. The study species we selected were those most frequently observed in the study site, and which had enough detections to converge with the occupancy and detection rate models. The study species we investigated included five mammals and one large ground-dwelling bird: white-tailed deer (*Odocoileus virginianus*), eastern gray squirrel (*S. carolinensis*), northern raccoon (*P. lotor*), coyote (*Canis latrans*), Virginia opossum (*Didelphis virginiana*), and wild turkey (*Meleagris gallopavo*), henceforth referred to as deer, squirrel, raccoon, coyote, opossum, and turkey.

2.1. Study area

This study took place in Stone Mountain State Park, located in the foothills of the Appalachian Mountains in North Carolina, southeastern USA. This 57-km^2 protected area was in a rural area and contained occupied homesteads until the late 1960s, when it was designated as a protected area. The 2.6-km study trail was a 2-m wide equestrian trail built using motorized machinery from February 6th through June 5th, 2015, and opened to recreational use on June 6th, 2015. The study trail was located at a minimum distance of 275 m from existing trails and 460 m from existing roads or other park infrastructure. The trail zone was located at elevations ranging from 463 to 578 m above sea level (NC OneMap, 2014). The control zone was located in an area with a similar ecosystem, at least 575 m from existing trails and roads, and elevations ranging from 454 to 628 m above sea level. Both trail and control zones were within Eastern North American Cool Temperate Forest, dominated by Southern and Central Appalachian Oak Forest (USGS, 2014). No hunting was permitted within the protected area. Both the trail and control zones were 2.6 km long, surrounded by a 50 m expected zone of influence, making each site 13 ha. The location of the trail and control zones are shown in Fig. 1.

Trail building took place during daylight hours (see Fig. 2). Trail design and building were carried out in accordance with the International Mountain Biking Association (IMBA) sustainable trail building guidelines (Felton, 2004), which are widely used in the sustainable design of a variety of recreational trail types. Trail construction required removal of understory and some small trees along the 2-m wide path. Motorized equipment was used to build the trail, including chain saws, leaf blowers, all-terrain vehicles, excavators, and compactors. In one area, rocks were removed using explosives. To minimize erosion, leaf blowers were used to cover exposed soils on the downhill slope along the trail with leaves as the trail was built, as required by the North Carolina Department of Environmental Quality. Gravel was used on the path in some zones particularly susceptible to erosion.

2.2. Study design

Data were collected during three phases: before trail building (August 30th, 2014 – February 5th, 2015), during trail building (February 6th – June 5th, 2015), and after the trail was completed and open to recreational use (June 6th – September 12th, 2015). Sixty-three sampling points were located across three zones, with each zone containing 21 sampling points: (1) along the study trail, (2) in a near-trail corridor located 25–50 m on either side of the study trail, and (3) in a control zone. The near-trail corridor zone was determined from results in similar ecosystems showing some effect of trail-based recreational activity at a distance of 50 m from the trail, while no effect on wildlife occupancy or visit frequency was found at a distance of 200 m from the trail (Kays et al., 2016). To conduct occupancy analysis, this number of sampling points is recommended by some wildlife researchers (Kays et al., 2016; Si, Kays, & Ding, 2014) but is fewer than the number recommended by others (Rovero, Zimmermann, Berzi, & Meek, 2013). As this is a relatively small study zone, we defend the use of this number of sampling points as representative of the study area.

On-trail sampling points were randomly selected and established at an interval of 125 m along a 2600-m section of the proposed trail, which was previously delineated by park staff with markers at the site and mapped using a Global Positioning System (GPS) unit. Near-trail sample points were determined by drawing a line perpendicular to the trail at each on-trail point, then placing a point on a randomly selected side and distance from the trail within the 25–50 m near-trail zone. Slight alterations were made to this randomization process to ensure that each point was located at an appropriate slope and minimum dis-

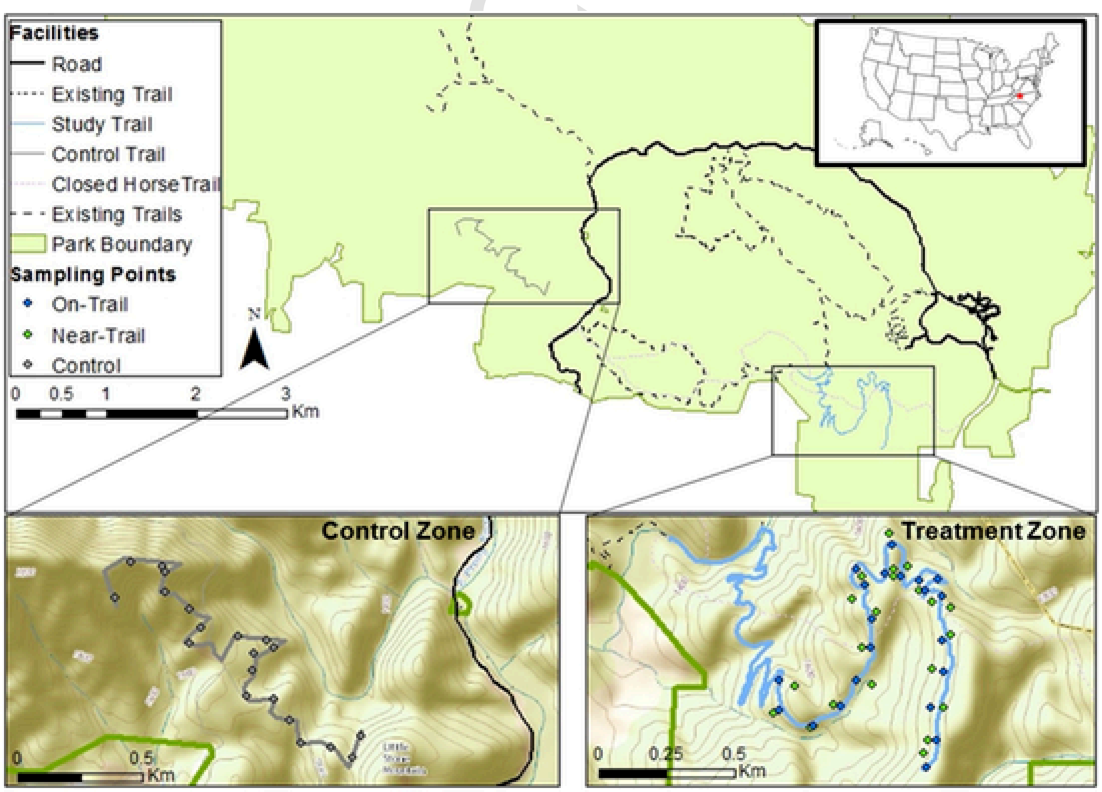

Fig. 1. Map of the study site in the southern portion of Stone Mountain State Park. Sampling point locations are marked in insets: control zone (left) and treatment zone (right). Location of the protected area within the USA is indicated with the red point in the inset in the top right corner (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

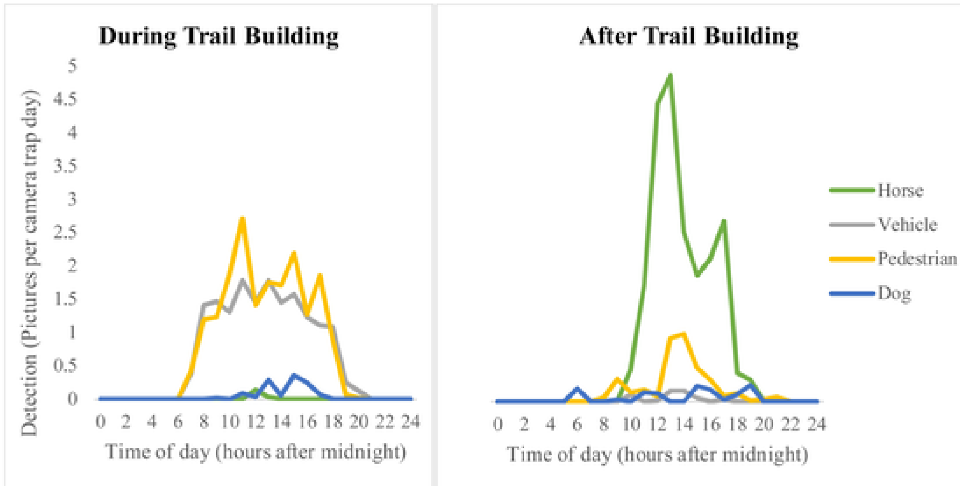

Fig. 2. Daily timing of human on-trail activity during and after trail building. During trail building, nearly all pedestrian activity was the trail construction crew. Before trail building, only five pedestrians were detected during the six-month period.

tance of 25 m from all sections of the trail, specifically in sections where the trail contains multiple switchbacks.

The control zone was selected using topographic, geologic (NC OneMap, 2014), vegetation (USGS, 2014), and park infrastructure and boundary maps (unpublished data provided by the North Carolina Department of Parks and Recreation) using ArcMap 10.1, and located at a distance of approximately 2.5 km from the study trail. In the control zone a 2.6-km line was drawn to correspond with the slope and elevation range of the 2.6-km study trail. Control zone sampling points were determined along this line using the same method as the on-trail sampling points (Fig. 1).

2.3. Data collection

All field data were collected using motion-triggered field cameras, henceforth referred to as camera traps, a widely used and relatively non-invasive method in wildlife studies (Kays et al., 2011; McCallum, 2013; Rovero et al., 2013). Cameras used in the study were Bushnell TrophyCam HD, a camera with a rapid trigger that is often used in wildlife monitoring, with an infrared flash for recording photos at night with minimal disturbance to wildlife (Rovero et al., 2013). At each sampling point, a camera was attached to the nearest tree of appropriate size at knee-height from the ground (approximately 0.5 m). Cameras were oriented towards an open area with a relatively flat slope, with lenses angled parallel to the slope of the ground. In rare occurrences, nearby vegetation or underbrush was cleared to improve camera performance. On-trail cameras were oriented along the trail to maximize the trail-based activity detected (Miller, Leung, & Kays, 2017). These procedures are typical for studies using camera traps for wildlife data collection (Erb, McShea, & Guralnick, 2012; Meek et al., 2014; Rowcliffe, Carbone, Jansen, Kays, & Kranstauber, 2011; TEAM Network, 2011). In the 20 m by 20 m area surrounding each data collection point, we recorded the vegetation species present, openness of landscape, elevation, and relative slope of the area. Representation of these microhabitat characteristics were consistent across all zones, leaving no reason to believe that differences in wildlife activity between zones might be due to microhabitat effects.

We deployed seven cameras in each study zone for a period of three weeks, placing a camera at every third established sampling point. Thus, the points being sampled at any one time were spaced at approximately 375 m along the trail. After typically three weeks (range: 19–38 days, mean: 23.5 days), we exchanged memory cards and batteries and moved each camera to the next sampling point sequentially, allowing all 21 points in each zone to be sampled in a total of nine weeks.

Trail building start and end dates were used to define the phase for all cameras, regardless of their position along the trail. This was done because the initial building-related disturbance of trail clearing, involving several crew members and motorized equipment such as chain saws occurred within the first few days of this phase along the entire length of the trail.

We programmed cameras to take three photographs per trigger with a delay of one second between trigger events and no delay between retriggering. Photos were aggregated into sequences separated by at least one minute between camera triggers to minimize repeated observations of the same individual while maximizing observations of independent events of species appearances (Yasuda, 2004). We recorded presence and detection rate (number of detections per day) for each animal species. We also recorded human activity on cameras. We attained approval from the Institutional Review Board, and maintained privacy by not identifying individuals in photos, and not circulating photos of people outside of the research group. In most photos, individuals were not identifiable due to the low location of the cameras and the low resolution of the photos (Miller et al., 2017). We used the eMammal photo management system (McShea, Forrester, Costello, He, & Kays, 2016) and archived all pictures and data at eMammal.org.

2.4. Data analysis

We performed descriptive analyses to determine the number of photos, sequences, effort, species observed, and type of human activity observed (trail crew on motorized vehicle, trail crew on foot, or recreationist). For human activity, we plotted the type of activity and time of day at which it occurred, on average, during and after trail construction. We quantified sampling effort as the number of camera trap days: number of camera traps deployed times the number of days deployed. The relative number of species detected was quantified by multiplying the number of species observed in each zone and phase by the effort in that zone and phase, then dividing by the average effort across all zone and phase combinations.

To address our research question and hypotheses, we analyzed three dependent variables: (1) occupancy probability, (2) detection rate, and (3) daily activity patterns for each of the treatment phases and both treatment zones. Occupancy probability measures the probability that a site (camera location in this case) is *occupied* by a given species. This analysis is based on binary detection/non-detection data, incorporates probabilities of false-negative detections, and accounts for imperfect detection through a hierarchical model framework (MacKenzie et al., 2006). Occupancy probability is represented by the Psi coefficient, which ranges from 0 to 1. Detection rate is a measure of the frequency with which each zone is *visited* by a species, based on rate of observation by the cameras. These two measures are complementary, with occupancy quantifying the spatial distribution of a species while detection rate describes habitat preference in the study area (Kays et al., 2016).

For occupancy and detection rate we performed contrasts, a method common in BACI studies, to answer the research questions regarding the effect of trail building and trail presence on terrestrial wildlife species in on-trail and near-trail zones, and tested for significance at $\alpha = 0.05$. For both analyses, a survey consisted of one camera trap day, with sampling occurring continuously throughout the 24 -h period starting and ending at midnight. To determine if sampling points were independent, we tested for spatial autocorrelation with Moran's I, using the 'ape' package in R (Paradis, Claude, & Strimmer, 2004). Using this test, a p-value smaller than 0.05 indicates spatial clustering of the data.

The effect of trail-building and trail presence on the occupancy probability for each study species was determined using single-species, single-season occupancy analysis run in Program MARK (MacKenzie et al., 2006; White & Burnham, 1999) through the 'RMark' package in R (Laake, 2013). We considered zone and phase as grouping variables and occupancy covariates, and detection distance and season as detection covariates. Detection distance was measured each time a camera was set, by measuring the distance from the camera at which movement of one researcher was detected, in meters (mean = 15.4 m); all animals observed are assumed to be within this distance from the camera. Season was defined as a categorical variable corresponding to the season (spring, summer, fall, or winter) in which the sampling period began. For each study species, we assessed the significance of the zone*phase interaction term in the occupancy model to determine if the change in a species' occupancy probability between pre-building and treatment phases (during and after trail building) were significantly different in the treatment zones (on-trail and near-trail) as compared with the same period in the control zone. We also calculated the odds ratio and 95 % confidence intervals to compare the change in occupancy odds between phases by site.

We determined the effect of trail building and trail presence on the detection rate for each study species using a zero-inflated Poisson regression on the count of detections for each species per survey, due to the dispersion and high proportion of zero values in our data. We tested for goodness of fit using the Vuong test to determine which species fit the zero-inflated Poisson regression analysis (Vuong, 1989). This test showed that the zero-inflated Poisson regression model fit five of the six study species significantly better than did the ordinary Poisson regression model. We thus proceeded with analysis of these five species: deer, squirrel, raccoon, coyote, and turkey. We used the same covariates in this analysis as in the occupancy model (detection distance, season and a zone-phase term for both "count" and "zero" portions of the model). Analyses were conducted in R, using the 'pscl' package for zero-inflated Poisson regression (Jackman, 2015; Zeileis et al., 2008), and 'lsmeans' package (Lenth, 2015) to calculate least square means, combining "count" and "zero" model coefficients. Significance testing was performed using the contrast of least square means to answer our research questions regarding the effect of trail building and trail presence on the detection rate in on-trail and near-trail zones.

We also compared the daily activity patterns of each study species across zones and phases. After first converting all observation times to the time relative to sunrise and sunset (see Nouvellet, Rasmussen, Macdonald, & Courchamp, 2012 for methods), we used bootstrapping (10,000 samples) to calculate the difference between the treatment and control zone for each study species in relation to time, within the phases during and after trail building. For those species that had significantly different level of activity in the treatment zone compared with the control zone (based on a Wald test), we estimated the percent of overlap between control and treatment zones, using a randomization test of the probability that two sets of circular observations come from the same distribution (Ridout & Linkie, 2009). This analysis was performed in R, using packages 'activity' (Rowcliffe, 2019) and 'overlap' (Ridout & Linkie, 2009).

3. Results

We quantified the number of species observed, occupancy probability, and detection rate from 289,594 photographs containing 17 native mammal species and one large terrestrial bird species across all three zones (Table 1). In total our data consisted of 8730 discrete wildlife detections at 301 sampling deployments (deployment refers to a camera set for a 3-week period), with a total of 7045 camera trap days of survey effort across all zones.

Human use of the trail was exclusively diurnal, and consisted primarily of construction workers and their vehicles during the trail building phase, and equestrian recreation after construction was complete (Fig. 2). In the on-trail zone during trail construction, there were an average of 16 passes per day by trail crew members on motorized vehicles (e.g. ATV, excavator) and 19 passes per day by trail crew members on foot. Once construction was complete, the trail had an average

Table 1
Full list of species observed in the study, camera detections in each of the three zones of the project per unit of effort (i.e. camera trap day), and total number of detections for each species. The table is organized in order from most to least total detections per species.

		Detections per camera trap day, by zone			Camera Detections
Common Name	Scientific Name	Control	On-Trail	Off-Trail	Total detections
White-tailed Deer	*Odocoileus virginianus*	1.0216	0.6330	0.9266	5872
Eastern Gray Squirrel	*Sciurus carolinensis*	0.1293	0.1189	0.2393	1121
Northern Raccoon	*Procyon lotor*	0.0624	0.1095	0.1449	755
Coyote	*Canis latrans*	0.0579	0.0288	0.0284	260
Wild Turkey	*Meleagris gallopavo*	0.0377	0.0236	0.0225	192
Virginia Opossum	*Didelphis virginiana*	0.0322	0.0136	0.0248	157
Unknown Mouse or Rat	*NA*	0.0332	0.0024	0.0138	103
American Black Bear	*Ursus americanus*	0.0221	0.0045	0.0110	81
Striped Skunk	*Mephitis mephitis*	0.0267	0.0024	0.0064	74
Bobcat	*Lynx rufus*	0.0111	0.0049	0.0055	48
Eastern Cottontail	*Sylvilagus floridanus*	0.0146	0.0000	0.0005	30
Southern Flying Squirrel	*Glaucomys volans*	0.0045	0.0014	0.0018	17
Grey Fox	*Urocyon cinereoargenteus*	0.0030	0.0014	0.0009	12
Red Fox	*Vulpes vulpes*	0.0010	0.0000	0.0005	3
Eastern Spotted Skunk	*Spilogale putorius*	0.0000	0.0003	0.0005	2
Eastern Fox Squirrel	*Sciurus niger*	0.0000	0.0003	0.0000	1
Long-tailed Weasel	*Mustela frenata*	0.0000	0.0000	0.0005	1
Woodchuck	*Marmota monax*	0.0000	0.0003	0.0000	1
Grand Total		1.4575	0.9454	1.4278	8730

of 1.4 visitors passing per day; this number indicates low use of the trail, perhaps because it was not widely known to the public. In near-trail and control zones, nearly zero human activity occurred during the project.

3.1. Variation in the control zone

Before describing the results for each species, it is important to note that variation existed across all zones, including the control zone, across the three phases of the project (i.e. before, during, and after trail building). This variation is likely due to seasonal changes in the study species' activity levels. The 'before' phase occurred over late summer, fall and early winter, the 'during' phase spanned late winter and spring, and the 'after' phase included late spring and summer (see Section 2.2 for exact dates of each phase). Investigating the data from our control zone shows that turkeys were most active in the 'before' phase (i.e., fall and winter months), deer and coyotes were most active in the 'during' phase (i.e., late winter and spring months), and squirrels, raccoons, and opossums were most active in the 'after' phase (i.e., late spring and summer months). These peak activity periods generally correspond with seasons during which each species has young with which females forage for food, which likely explains the higher levels of occupancy and detection rates found in the control zone.

These control zone data are critical in separating the effects of trail building from seasonal effects. We continue by reporting the results of occupancy, detection rate, and daily activity pattern of each study species in relation to the data from the control zone. We conducted occupancy analyses for the five species that had adequate detections for model convergence: squirrel, raccoon, coyote, turkey, and opossum. For these five species, we analyzed the effect of trail building (i.e. the 'during' phase) and trail presence (i.e. the 'after' phase) in each treatment zone (i.e. on-trail and near-trail zones) in relation to the control zone (Fig. 3). Next, we analyzed the detection rate for five species that had adequate detections for convergence with the zero-inflated Poisson regression model: deer, squirrel, raccoon, coyote, and turkey. For these species, we analyzed the effects of trail building and trail presence in both on-trail and near-trail zones using contrast equations on the least square means of detection rate resulting from these species' regression models (Fig. 4). Finally, we analyzed the daily activity patterns of each of the six study species, looking for significant differences between each treatment zone and the control zone, both during and after trail building (Fig. 5). For each of the six species, results are summarized below and in Table 2. For each species, we present all results on the effects of trail building, followed by all results on the effects of trail presence.

3.2. White-tailed deer

Deer occupancy was equal to one in several zone-phase data sets, making it impossible to answer our research questions using occupancy analysis due to lack of variation (Welsh, Lindenmayer, & Donnelly, 2013). However, the data supported significant effects of trail building on deer in the near-trail zone (Table 2). Deer detection rate decreased by 41 % during trail building in the near-trail zone, compared with the control zone ($P \leq 0.001$) (Fig. 4; Table A2, Appendix A). Deer daily activity patterns in the on-trail zone did not differ significantly from those in the control zone. However, daily activity patterns during trail building in the near-trail zone were significantly different from those in the control zone ($P < 0.05$, difference of 27 %). In the near-trail zone, deer had reduced activity density peaks around dusk and dawn, accompanied by a smaller activity peak around noon in the near-trail zone as compared with the control zone (Fig. 5a). Corresponding human activity patterns are shown in Fig. 5d for comparison. We found no significant effect of trail presence on deer detection rate or daily activity patterns.

3.3. Eastern gray squirrel

We found no significant effects of trail building on squirrels (Fig. 3; Fig. 4; Tables A1 and A2, in Appendix A). However, the data supported significant effects of trail presence on squirrels in the on-trail zone (Table 2; Table A2 in Appendix A), with squirrel detection rate decreasing by 93 % in the on-trail zone after trail building, compared with the control zone (Fig. 4). After trail building was complete, squirrel daily activity patterns in both on-trail and near-trail zones were significantly different from those in the control zone (difference from the control zone of 13 % and 17 %, respectively) ($P < 0.05$) (Fig. 5). Squirrels had larger activity peaks just after dawn in both treatment zones as compared with the control zone (Fig. 5b and c). Fig. 5d shows human activity patterns for comparison.

3.4. Northern raccoon

Trail building corresponded with a significant increase in raccoon occupancy and detection rate in the on-trail zone (Table 2). In the control zone, raccoon occupancy was 0.609 before trail building and dropped to 0.283 during trail building, with a decrease in the occupancy odds (odds ratio: 0.254, 95 % CI: 0.085, 0.758). Meanwhile, in the on-trail zone raccoon occupancy increased from 0.772 to 0.922, with an increase in the occupancy odds (odds ratio: 3.507, 95 % CI: 0.514, 23.916) (Fig. 3; Table A1, Appendix A). This difference was reflected in the interaction term for zone and phase, which was significantly different from zero (2.63, 95 % CI: 0.429, 4.822, $P \leq 0.001$). During trail building, the occupancy odds ratio increased enormously in the on-trail zone, reaching 1,382 % (95 % CI: 153.6 %, 1,242.5 %) of the occupancy odds ratio for the control zone. The raccoon detection rate also supported significant effects of trail building for raccoons along the trail (Fig. 4; Table A2 in Appendix A). In the on-trail zone, raccoon detection rate increased by 17 % during trail building ($P \leq 0.001$) compared with the control zone. Raccoons did not demonstrate significant differences in daily activity patterns between the control and treatment zones. In our study site, raccoons were active almost exclusively at night, when there was no human activity at the site. We found no significant effect of trail presence on raccoon occupancy, detection rate, or daily activity patterns.

We recognize that spatial autocorrelation exists within the occupancy results for raccoon. Spatial autocorrelation, which indicates a lack of independence between sampling points, can lead to an overestimated precision in occupancy estimates (Legendre, 1993) and increase the risk of Type I error, but is often not considered (Poley et al., 2014). Additionally, the agreement between the occupancy and detection rate results supports the significant effect of trail building on raccoons in the on-trail zone.

3.5. Coyote

Our results suggest that trail building resulted in a small but significant decrease in coyote occupancy and detection rate in the near-trail zone (Table 2). In the control zone, coyote occupancy was 0.612 before and rose to 0.671 during trail building, resulting in a slight increase in the occupancy odds (odds ratio: 1.293, 95 % CI: 0.361, 4.641). Meanwhile, in the near-trail zone, coyote occupancy decreased from 0.551 to 0.117, resulting in a substantial decline in the occupancy odds (odds ratio: 0.108, 95 % CI: 0.024, 0.445) (Fig. 3; Table A1, Appendix A). The interaction term for zone and phase was significantly different from zero (−2.48, 95 % CI: −4.390, −0.576, $P \leq 0.001$).

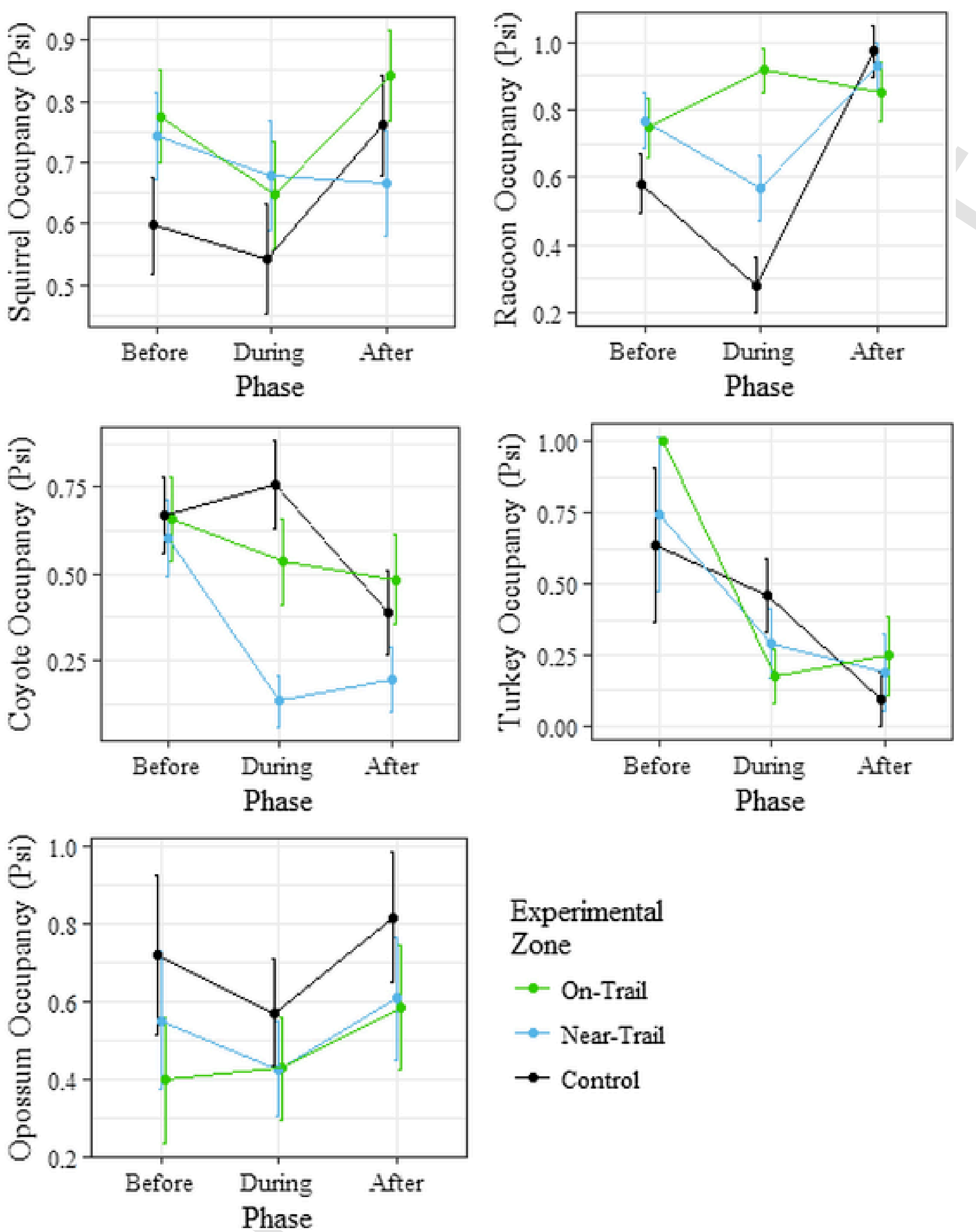

Fig. 3. Occupancy probability (Psi) model estimates for each zone-phase combination for each of five study species. Error bars show standard error; points for which error bars do not overlap are statistically different, at the alpha = 0.05 level. Significant relationships include: Raccoon occupancy increased along the trail during trail building and Coyote occupancy decreased near the trail during trail building.

The occupancy odds ratio declined slightly in the near-trail zone to 8% (95 % CI: 1.2 %, 56.0 %) of the occupancy odds ratio for the control zone.

Our detection rate analysis also supported significant effects of trail building for coyotes both along the trail and in the near-trail zone (Fig. 4; Table A2 in Appendix A). During trail building, coyote detection rate decreased by 6 % on-trail and 7 % in the near-trail zone, compared with the control zone ($P \leq 0.05$). Coyotes did not demonstrate significant differences in daily activity patterns between the control and treatment zones. In our study site, coyotes were active almost exclusively at night, with the exception of a small activity peak around noon in the control zone that was absent in both treatment zones, after trail building was complete. We found no significant effect of trail presence on coyote occupancy, detection rate, or daily activity patterns.

3.6. Wild turkey

The data did not support significant effects of trail building or trail presence in either treatment zone for turkeys, including all three analyses (Table 2; Tables A1 and A2, Appendix A). This species did not appear frequently enough to allow statistical analysis regarding daily activity patterns. However, turkeys are diurnal and thus might have undetected responses to trail building or presence.

3.7. Virginia opossum

The data did not support significant effects on of trail building or trail presence in either treatment zone for opossums occupancy, detection rate, or daily activity patterns (Table 2; Tables A1 and A2, Appendix A). In our study site, opossums were active almost exclu-

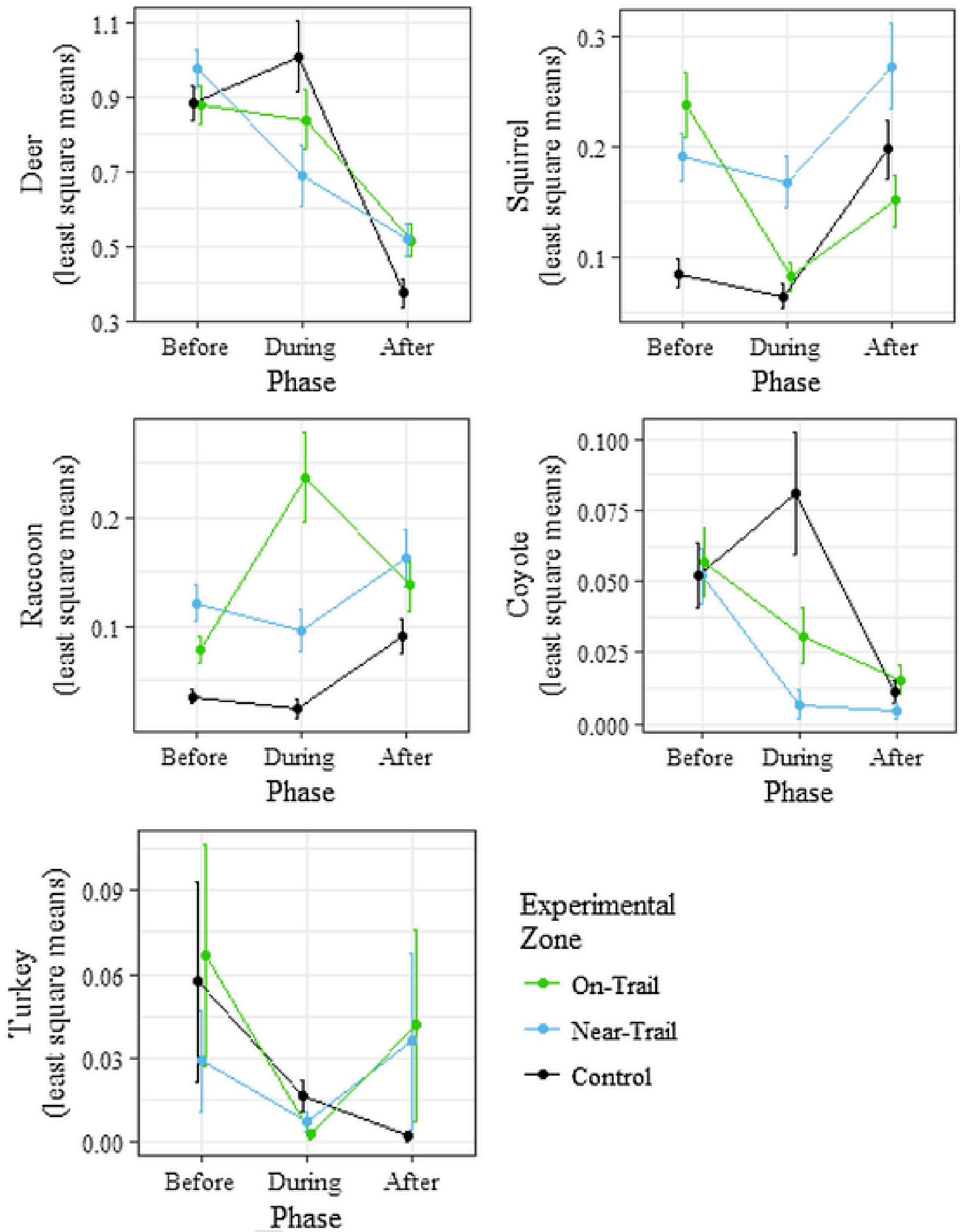

Fig. 4. Detection rate for each zone-phase combination for each of five study species. Least square means (y-axis) is calculated from the "count" and "zero" portions of the zero-inflated poisson regression model. Error bars show standard error; points for which error bars do not overlap are statistically different at the alpha = 0.05 level. Significant relationships include: Deer detection rate decreased in the near-trail zone during trail building, squirrel detection rate decreased along the trail after trail building, raccoon detection rate increased along the trail during trail building, and coyote detection rate decreased along and near the trail during trail building.

sively at night, when the trail construction crew and recreationists were absent.

4. Discussion

Trails are an important recreational infrastructure common to nearly every protected area. Because trails occur within spaces designated to conserve and protect wildlife species, understanding their effects on wildlife is important in the goal of wildlife conservation. Although trail construction and maintenance occur frequently within protected areas, the effects of these practices on wildlife are not well understood. This study establishes a method to evaluate the impacts of trail construction and trail presence on common wildlife species, using camera traps as part of a BACI experiment. Our results are supported by previous studies investigating the effects of trail presence and a range of human recreational activities on common species across larger spatial scales, focusing here on the effects of trail building. Our findings that four of the six species studied demonstrated changes in activity during and/or immediately after trail construction underscores the importance of considering the extent and timing of trail building projects to minimize negative impacts on local animal populations.

Our results indicate that effects on the study species were strongest during trail building but such effects dissipated once trail building was complete. Through analysis of detection rate, we found that trail construction corresponded with raccoons increasing their use of the on-trail zone, deer using the near-trail area less frequently, and coyotes slightly decreasing their use of both on-trail and near-trail areas. These results suggest that raccoons are attracted to the disturbance of the trail construction zone while deer and coyotes avoid the immediate area, with the zone of influence reaching at least 50 m from the trail for deer and coyotes. Only one species, squirrel, showed significant response

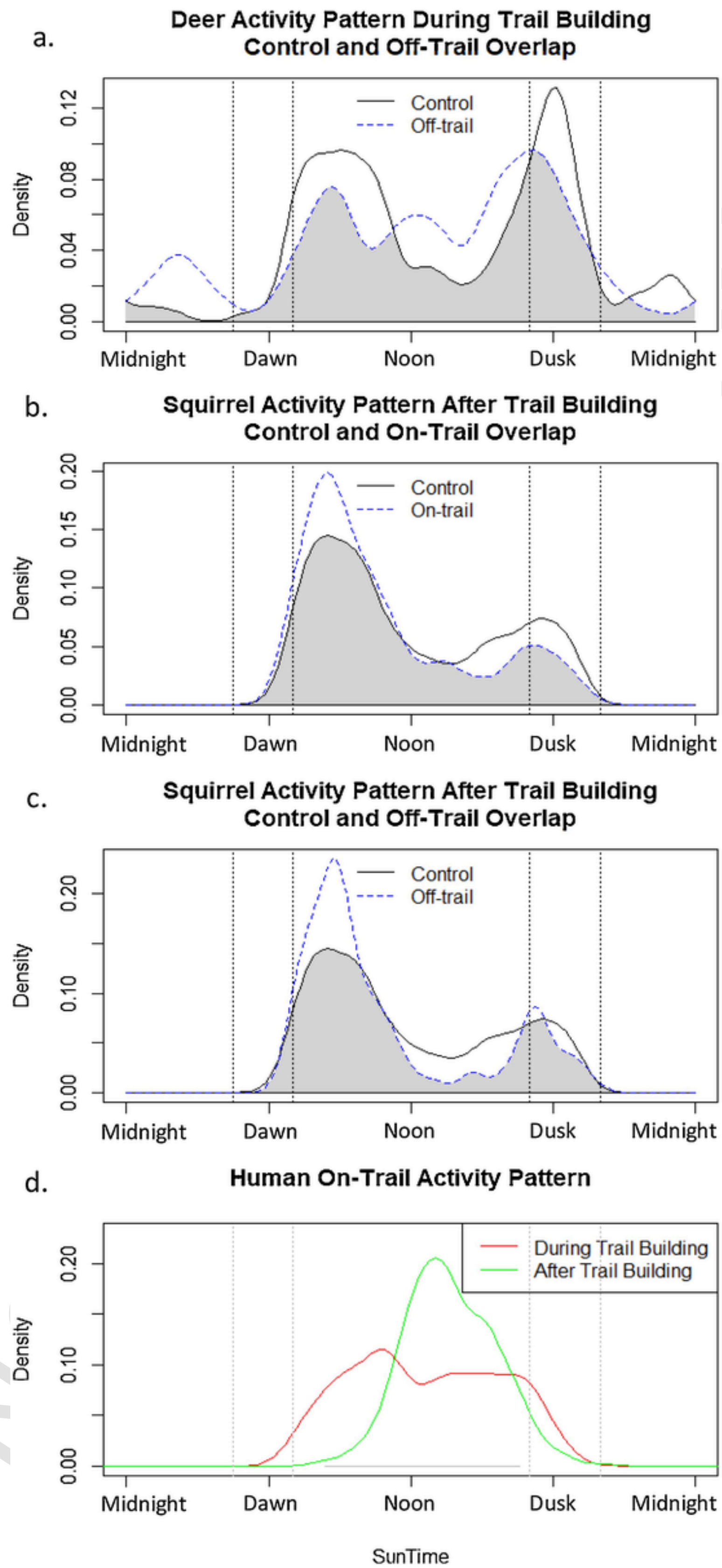

Fig. 5. Daily activity patterns for deer, squirrel, and humans, represented through the density of observations over time, relative to sunrise (i.e SunTime). For deer and squirrels, activity patterns are shown during the periods when their activity was significantly different from the control zone. Human activity patterns include the trail building crew and recreationists. Researchers' activity is excluded from the presentation of human activity as it is constant in all zones and phases.

Table 2
Summary of the results of our three statistical analyses: occupancy, detection rate, and activity pattern. All significant results are described with the direction of the result; "X" indicates no significant differences from the control zone.

Analysis	Species	Results, percent difference from control site			
		During Trail Building		After Trail Building	
		On-Trail	Near-Trail	On-Trail	Near-Trail
Occupancy,% difference in occupancy odds ratio from control zone	Deer	X	X	X	X
	Squirrel	X	X	X	X
	Raccoon	Increase, 1382 %	X	X	X
	Coyote	X	Decrease, 8 %	X	X
	Turkey	X	X	X	X
	Opossum	X	X	X	X
Detection Rate, % change from control zone	Deer	X	Decrease, 41 %	X	X
	Squirrel	X	X	Decrease, 93 %	X
	Raccoon	Increase, 17 %	X	X	X
	Coyote	Decrease, 6 %	Decrease, 7 %	X	X
	Turkey	X	X	X	X
	Opossum	X	X	X	X
Daily Activity Pattern, % overlap with control zone	Deer	X	Spread throughout day, 27 %	X	X
	Squirrel	X	X	Avoid recreational activity, 13 %	Avoid recreational activity, 17 %
	Raccoon	X	X	X	X
	Coyote	X	X	X	X
	Turkey	X	X	X	X
	Opossum	X	X	X	X

to trail presence after construction, decreasing use along the trail itself by 93 % according to detection rate by our cameras.

Effects of trail construction on species occupancy paralleled the results of the detection rate analysis, but were less profound. This indicates that the study species' responses to trail building were more substantial at the level of habitat use intensity than that of geographic distribution. Raccoons and coyotes had significant changes in occupancy during trail building compared with our control zone and measurements of the same site before construction. These observations were consistent with changes in these species' detection rates, and suggest a pattern of displacement (coyote) and habitat expansion (raccoon) resulting from trail building. However, these effects were temporary, with occupancy returning to levels similar to those in the control zone after trail building was complete. If prolonged, this type of response could lead to human-mediated predator shelter or attractive sinks, as found in previous studies (Hebblewhite & Merrill, 2007; Muhly et al., 2011; Roever, Boyce, & Stenhouse, 2008; Shannon et al., 2014). It is important to note, however, that our study trail received relatively low use once it was open to the public, with an average of only 1.4 visitors passing per day; our results might not be indicative of trails with higher use levels.

Analysis of the daily activity patterns of our study species suggest that deer and squirrels avoided human activity in real time. Both of these species are active during daytime hours, when human activity is highest. In the study area, deer typically had crepuscular and diurnal activity, while squirrels were primarily diurnal. Both species' activity patterns shifted to avoid peak times of human activity, as discussed in further detail below. Raccoons, coyotes, and opossums, which are all primarily nocturnal within our study site, did not show significantly altered daily activity patterns in the treatment zones. Although turkeys had too few detections to analyze statistically, it is worth noting that this primarily diurnal species appeared only three times along the trail during trail building – once each at dawn, noon, and dusk. These results suggest that species which are primarily diurnal are more highly affected by daytime trail-based human activity. Altered daily activity patterns in response to human activities is well documented in mammals, including coyotes, gray foxes, mule deer, (Nix et al., 2018; Reilly et al., 2017), black bear, white tailed deer, elk, and wolves (Barrueto et al., 2014; Rogala et al., 2011), most of which are primarily or partially diurnal species.

4.1. Population-level implications by species

Raccoons were the only species to increase their use of either treatment zone during trail building, having increased detection rate in the on-trail zone by 17 %. Primarily nocturnal, raccoons were temporally separated from daytime human activity during trail building. Raccoons are known to be attracted to point sources of human disturbance and often use edge habitat (Barding & Nelson, 2008), and were likely attracted to loosened soil for forage, as well as novel objects or food scraps left along the trail overnight. These two factors explain why the raccoon detection rate increased along the trail during construction. Our results showed that the raccoon detection rate returned to levels similar to those observed in the control zone after trail building was completed. This observation indicates that raccoons do not disproportionately use trails, consistent with previous findings (Gompper et al., 2006; , J.R. Miller and Hobbs, 2000; Kays et al., 2016).

The coyote detection rate decreased slightly both along the trail and in the near-trail zone during trail building (5.5 % and 7.4 %, respectively). These results suggest that coyotes avoided the on-trail and near-trail zones during high-intensity trail building activity. Coyotes have been observed to be leery of human presence and novel objects (Young, Mahe, & Breck, 2015), typical of the trail construction zone. White-tailed deer, a main source of food for coyotes (Crimmins, Edwards, & Houben, 2012), also showed decreased activity in the on-trail zone during trail building, which could have resulted in less motivation for the coyotes to visit the trail area during this project phase. Coyotes are also widely known to inhabit human-influenced spaces such as suburban areas (Way, Ortega, & Strauss, 2004; Weckel, Mack, Nagy, Christie, & Wincorn, 2010), consistent with our observation that coyote activity returned to levels similar to those observed in the control zone after trail building was complete.

Deer were by far the most common species captured by cameras in this project. Deer occupancy was equal to one in several zone-phase data sets, making it impossible to answer our research questions using occupancy analysis due to lack of variation (Welsh et al., 2013). Our detection rate data showed that deer used the near-trail zone 41 % less frequently during trail building, the period in which near-trail human activity was most frequent. This decrease is further explained through altered daily activity patterns, which suggested that deer avoided periods of peak human activity. This result is consistent with previous findings that near-trail activity resulted in greater impacts on deer than did more predictable on-trail activity (Miller, Knight, & Miller, 2001). Furthermore, deer activity in the near-trail zone was spread more evenly throughout the daylight hours during trail building than it was at the same time in the control zone. Deer in this previously undisturbed area might be confused by the sudden occurrence of human activity, changing their daily activity patterns and shifting their use of habitat. However, deer are very common in this area and their conservation is not a concern at this time.

Squirrels were the only species that showed a significant effect from trail presence after construction, with its detection rate decreasing by 93 % on the trail once trail building was complete. A diurnal species, squirrel daily activity patterns shifted away from peak periods of human activity along the trail. We suggest that this decrease could be due to (1) avoidance of humans and/or (2) increased perceived predation risk. Squirrels with less exposure to humans have been found to flee human approach from further distances (Engelhardt & Weladji, 2011). In our study site, squirrels had very low exposure to humans prior to trail building. If human avoidance is the driving factor, squirrel use of the trail might increase over time as the species becomes habituated to humans (see Kays et al., 2016). However, decreased use of the trail zone by squirrels may also be due to an increased perceived predation risk in this open area. If predation risk is driving the decrease in squirrel activity, we expect that squirrels will be displaced from the trail zone in the long-term.

We found no significant changes in the occupancy, detection rate, or daily activity patterns for wild turkeys. This species is a habitat generalist and has been found to benefit from a heterogeneous landscape structure (Rioux, Bélisle, & Giroux, 2009). Most previous studies have associated recreational activities with negative impacts on birds (Steven, Pickering, & Guy Castley, 2011), including reduced intensity of habitat use for grouse (Rösner, Mussard-Forster, Lorenc, & Müller, 2013). If similar effects are present in our study site, they were not detected using our methods.

Virginia opossums also did not show significant effects on occupancy, detection rate, or daily activity patterns related to trail building or trail presence. Previous research on opossums found no significant impacts of anthropogenic influences such as trail use in the Appalachian ecosystem (Erb et al., 2012) and negative association with areas of bare earth in an urban setting (Sinclair, Hess, Moorman, & Mason, 2005). The trail in our study is unpaved, and would be considered bare earth during and in the first few months after construction. We did not detect these possible changes in opossum detection rate, suggesting that if present, these effects are too small to be detectable using our methods.

4.2. Community-level implications

Our results are consistent with those of a study in an overlapping region, in which recreational trail use was not a consistently significant predictor of any of twelve species' use across all sites (Kays et al., 2016). This study found patterns suggesting a human-mediated predator shelter effect of highly used trails, with raccoons, bears, turkeys, and bobcats avoiding heavily used trails (>100 people/day), while red foxes and gray squirrels used such trails more frequently than trails with lower human use levels. This pattern was also found for bears and red foxes in another Appalachian study (Erb et al., 2012). If human use of our study trail increases, similar patterns of human-mediated predator shelter might emerge in our study site, with a decreased presence of large predators such as coyotes and bobcats coinciding with increased presence of mesopredators (e.g. foxes) and prey species (e.g. squirrels and deer). However, it is also possible that prey species such as squirrels may continue to have decreased activity levels and altered daily activity patterns along the trail corridor, as seen during the first few months after trail construction in our study. Further data collection is needed to determine long-term effects of trail construction at both the population and community level.

Our analysis extended into the first three months after trail construction was complete, during which very few recreationists used the new trail, allowing us to investigate the effect of the trail structure on the local wildlife community. Our results indicate that impacts on the study species were almost entirely restricted to the trail building phase. Previous studies in the area have found non-motorized trail-based human recreation to have limited effects on wildlife (Kays et al., 2016). The present study expands on such research, as we collected data on wildlife activity before the trail was present in the landscape. The lack of impacts detected after trail building was complete is likely influenced by the low level of recreational activity on the trail. Future work investigating similar impacts on a higher use trail are recommended to further explore the effects of trail use on wildlife, a unique opportunity given the availability of data both before and after the trail was in place. Furthermore, such data can reveal if trail presence affects the species studied here in the long term, such as large predator species using the trail for movement during periods of low human trail-based activity, shifting the predator-prey balance, as seen in previous studies (Cusack et al., 2015; Harmsen et al., 2010; Karanth & Nichols, 1998).

The trail constructed during this project used a motorized approach, with equipment such as excavators, all-terrain vehicles, chain saws, leaf blowers, and motorized trail compactors. In our study, an average of 16 passes by motorized vehicle and 19 passes by trail crew members on foot occurred along the trail per day during construction. Previous research found that non-motorized recreation resulted in greater impacts to several wildlife species than did motorized recreation (Harris, Nielson, & Rinaldi, 2013; Kucera, 1976). However, a review found motorized recreation to displace a larger number of species over longer distances than did non-motorized recreation (Gaines, Singleton, & Ross, 2002). Future research regarding the difference between impacts of mechanized and manual trail construction would be an important contribution to management in designated Wilderness areas, where the use of motorized equipment is highly restricted.

4.3. Limitations

Although we detected a total of 17 mammalian species and at least four bird species, our analysis was limited to the six most common species in the study area, which were detected with enough frequency to fit the occupancy and/or detection rate analyses. However, rarer species detected less frequently might also respond to trail building and/or trail presence. Future research using different methods might reveal responses of certain sensitive species to trail building and presence. The context of our study is also important to keep in mind, in that the study area is not pristine. Existing recreational trails lie within 275 m of the trail site, and other park infrastructure such as roads lie within 460 m. Recreational activity was present along a logging road in the treatment area until 2008. Species with large home ranges or with a life span greater than 7 years may have already been habituated to human use. The results presented here are restricted to the study site and year. However, as most protected areas in which trails are built have nearby human activity, we believe that our study area is appropriate for the research questions, and that our results can inform future research and management.

Our study is restricted to short-term effects, with results indicating habitat reduction and expansion for two species during trail building, attraction and avoidance for three species during trail building, and avoidance for one species after the trail is open. To draw conclusions regarding habituation of species to the trail, longer-term monitoring data would be required. Additionally, our data span an entire year but has a relatively short period of overlap of only 14 days between years. Our results would be strengthened by having a longer overlap between pre-trail building and post-trail building data.

BACI designs are powerful in their inference but difficult to deploy with replication to study landscape ecology. In our case, we took advantage of an opportunity to use this gold standard scientific design to evaluate the effects of a single trail construction project. Our results are thus robust for this specific Appalachian application, but might be limited in their generality. However, given how our results fit within the growing literature on trail effects, we argue that our results are generally relevant and indicative of the impacts of trail building on wildlife species characteristic of the region. As the first study in a forested habitat investigating the effects of trail building on wildlife activity using an experimental design, we believe the method developed here will be instrumental in future studies investigating the impacts of building and presence of trails and other human-made linear corridors on wildlife in a range of ecosystems, as a pilot study or as a part of a meta-analysis. We encourage researchers to collaborate with protected area agencies to form natural BACI experiments such as the one presented here. Implementing this method along trail building projects in other locations would build a global array of studies, bringing to light both common and unique effects of trail building on a large variety of species. We also encourage researchers to use citizen science methods to implement larger scale versions of the work presented here, ideally continuing the work for several years after new trails are built. Such studies are important in protected areas where an expansion of human recreation is planned, or where the landscape is heavily fragmented by recreation, and will contribute critical knowledge regarding the effect of new trail construction on local wildlife. Additionally, in areas where endangered species and recreation overlap, a study modeled after ours could indicate whether recreation trails correspond with change in these protected species' behavior.

5. Management implications and conclusions

Trail construction affected four species in the on-trail zone, with two species showing responses up to at least 50 m from the trail. Although all of the species studied here were common in the study area, four of the six species studied were affected, suggesting that other species in other global locations are also likely to be affected by trail construction activities. In areas where conservation of endangered species is a concern, impacts of trail building could be reduced if managers restrict construction to a short time period and consider the life cycle of endangered species potentially affected by trail construction when determining the season in which construction will occur. Taking an example of one of our study species, coyotes den during the spring and are known to move den sites following human disturbance (Harrison & Gilbert, 1985). Trail building during the denning season could thus imply additional energy requirements from adults and make coyote pups more vulnerable to predation if den sites are moved. Furthermore, if endangered species are displaced during trail building, poorly timed construction could further threaten the species' local population.

Wildlife protection is an important part of protected area goals to conserve natural ecosystems while providing quality nature-based recreation opportunities. In this study, we presented our results of a natural experiment in the form of both general trends and inferential statistics. Such statistical results are scarce in natural and landscape-scale experiments, in which replication is often difficult, impossible, or impractical, yet recent discussion has led to more widespread support of such methods for the advancement of science (Colegrave & Ruxton, 2018; Davies & Gray, 2015; Oksanen, 2001). The research presented here, in combination with many previous studies investigating interactions of humans and wildlife in a rural setting, can inform science-based protected area management to minimize the negative impacts of recreation and associated infrastructure development. In our analysis we found that impacts of a new low-use trail, if any, are likely restricted to the immediate trail zone and limited to one of our study species, the Eastern gray squirrel. Highlighting the importance of minimizing trail construction impacts, our study supports the coexistence of wildlife and low-intensity recreation in southern Appalachian forests.

Ethical approval: All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Submission declaration and verification

The study is being submitted for exclusive consideration for publication as an article in *Journal for Nature Conservation*. Data and findings have not been published previously or submitted elsewhere for simultaneous consideration. The contents have been approved by all authors and by the responsible authorities in North Carolina State Parks, where the work was carried out. If accepted, the work will not be published elsewhere in the same form, in English or any other language, without consent of the copyright-holder.

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Appendix A. Further detail on occupancy and regression results

Table A1
Occupancy probability (Psi) for each study species in each treatment phase and zone. Psi coefficients are those of the zone*phase occupancy probability interaction term for each contrast equation, with corresponding standard error and p-value. The occupancy model contains p~Detection Distance + Season; Psi~Zone*Phase; group = Zone, Phase. Each contrast is performed only on data for the specific zones and phases required. Cells with "NA" indicate that the model did not fit the dataset for the site and zone for the corresponding species.

	During, on-trail			During, near-trail			After, on-trail			After, near-trail		
Species	Psi	SE	*P*	Psi	SE	*P*	Psi	SE	*P*	Psi	SE	*P*
Squirrel	−0.41	0.78	0.61	−0.09	0.76	0.91	−0.34	0.93	0.73	−1.06	0.75	0.16
Raccoon	2.63	1.12	≤0.001	0.30	0.83	0.73	NA	NA	NA	NA	NA	NA
Coyote	−0.90	1.02	0.39	−2.48	0.97	≤0.001	0.56	1.09	0.62	−0.65	0.97	0.51
Turkey	−3.33	3.15	0.30	−1.41	3.11	0.66	NA	NA	NA	NA	NA	NA
Opossum	1.42	2.55	0.59	0.03	1.64	0.99	0.34	1.41	0.82	−0.15	1.17	0.91

Table A2
Change in detection rate for the 5 study species during and after trail building in on-trail and near-trail zones, compared with the same change in the control zone, with model coefficient, standard error, and p-value. Detection rate equations included Zone-Phase + Detection Distance + Season covariates for both "count" and "zero" portions of the zero-inflated Poisson regression model.

	During, on-trail			During, near-trail			After, on-trail			After, near-trail		
Species	Coeff.	SE	*P*	Coeff.	SE	*P*	Coeff.	SE	*P*	Coeff.	SE	*P*
Deer	−0.16	0.12	0.18	−0.41	0.12	≤0.001	0.15	0.08	0.07	0.05	0.08	0.53
Squirrel	−0.03	0.05	0.50	0.00	0.03	0.93	−0.20	0.04	≤0.001	−0.03	0.05	0.50
Raccoon	0.17	0.05	≤0.001	−0.01	0.03	0.62	0.00	0.03	0.89	−0.01	0.03	0.65
Coyote	−0.06	0.02	≤0.05	−0.07	0.02	≤0.001	0.00	0.02	0.98	−0.01	0.01	0.64
Turkey	−0.02	0.03	0.45	0.02	0.03	0.53	0.03	0.04	0.48	0.06	0.05	0.17

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